THE ANATOMY OF TWO SPECIES OF HELICARION FROM TROPICAL AFRICA.
By Hugh Watson, M.A.
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Throvgh the kindness of Dr. Péringuey and Mr. K. H. Barnard, of the South African Museum, Cape Town, of Sir Sidney Harmer, K.B.E., and Mr. G. C. Robson, of the British Museum, and of Major M. Connolly, I have lately been given the opportunity of investigating the anatomy of two African species of Helicarion, an opportunity of which I am very glad to avail myself, seeing that so little is known about the Zonitidæ of Tropical Africa.

My description of H. gomesianus (Morelet) is based upon the examination of a single specimen belonging to the South African Museum, and kindly sent to me for dissection by Major Connolly, who informs me that its shell bears a very close resemblance to three shells of $H$. gomesianus from Pungo Andonga, Angola, which the late King of Portugal presented to the British Museum. The specimen was found at Pemba, a village or mission station in Northern Rhodesia, in what was formerly known as the Mashukulumbe country, about 120 miles north-east of Livingstone and some 30 miles north-west of the River Zambesi.

The second species is one of which several examples were presented to the British Museum in 1910 by Mr. F. J. Jackson, C.B., having been collected in British East Africa, " probably at Nairobi." Major Connolly considers that this species is probably one which has not yet been named. There can be no doubt that it differs from all those of which any part of the anatomy has been described, and it cannot be certainly identified with any of the species at present only imperfectly known from descriptions and figures of their shells. I am therefore regarding it as new to science.

## Helicarion gomesianus (Morelet). ${ }^{1}$ Pemba, Northern Rhodesia. Plate III.

Shell depressed, paucispiral, imperforate, yellowish-green, and extremely thin, the basal region being practically membranous. Spire slightly raised, suture rather deep, whorls three, rapidly expanding, rounded at the periphery, and crossed by fairly wellmarked lines of growth. Protoconch with microscopical spiral sculpture. ${ }^{2}$ Aperture large, oval, 12 mm . in breadth; peristome thin and simple. Altitude 6 mm .; breadth 15 mm .

[^0]Foot long and narrow, the hinder part laterally compressed but not keeled, the top being excavated beneath the shell but raised posteriorly in front of the large caudal mucous pore, which has the form of a vertically elongated slit. Sole truncate in front and rounded behind, tripartite by a pair of longitudinal grooves, the central area being equal in width to each of the lateral areas, excepting towards the hinder end, where it becomes narrower owing to the convergence of the longitudinal grooves, which meet at the extremity. Foot-fringe and lateral areas of sole crossed by numerous transverse grooves. Peripodial grooves well marked, bending upwards in front of the candal mucous pore; ciliated epithalium of foot-fringe extending on to the lower sides of the peripodial grooves. Rather irregular radial grooves occur on each side of the hinder part of the foot, where there is also a longitudinal brown band.

Head and Neck with well-marked lateral grooves; dorsal grooves ill defined; vertical facial grooves absent, the front of the head being covered with small rugæ. Genital opening in the right lateral groove on the side of the head, about 2 mm . from the right upper tentacle.

Pallial Lobes, comprising a pair of rather narrow, fingershaped shell-lobes, one on each side of the shell, and about 3 mm . long in a specimen preserved in alcohol; together with right and left, slightly granular, body-lobes-the right forming a wide triangular flap beneath the respiratory opening and the right shell-lobe, the left being very broad and extending uninterruptedly from the respiratory opening over the neck and along the left side of the animal to a point a little behind the origin of the left shell-lobe.

Dorsal Srin lining the shell opaque white, excent for some translucent vein-like markings above the albumen gland, and for the area over the lung, which is also translucent, like the skin of the concealed undersides of the whorls.

Lung short and somewhat wedge-shaped, being broad at the mantle-edge, but rapidly narrowing as it extends backwards. Roof of lung richly vascular, doubtless in order to compensate for the reduction of its area due to the encroachment of other organs normally occupying the spire. Main pulmonary vein coming towards the pericardium from the neighbourhood of the respiratory opening, but having numerous branches, including a large vessel from the left of the lung which unites with it close to the heart. Numerous short veins cross the narrow area to the right of the kidney, and these are mostly bordered with white.

Aorta dividing into two vessels soon after leaving the ventricle. The posterior passes backwards and then divides into two arteries which supply blood to the liver, etc.; the anterior bends round the loop of the intestine, gives off an artery to the salivary glands,
and then runs forwards towards the head, passing between the visceral and pedal ganglia.

Kidney sigmurethrous, somewhat cylindrical, being thick and rather narrow ; nearly 8 mm . long, and extending about 2 mm . in front of the heart. Primary ureter curved round at the anterior end, rather broad, and having its lining thrown into numerous thick, irregular, transverse folds of a light colour, contrasting strongly with the brown folds contained in the kidney itself. Secondary ureter containing much thinner transverse folds.

Pedal Gland embedded in the muscles of the upper part of the foot in the floor of the body-cavity, and extending back for a short distance in the solid hinder portion of the foot. Duct broad and rather flattened except at the posterior end, showing as a darker streak along the centre of the bottom of the body-cavity, from which it is only separated by a thin layer of transverse muscles. Roof of duct without folds; its floor with a pair of


Fig. 1.-Transverse section through the foot of Helicarion gomesianus (Morelet), showing structure of pedal gland, etc., $\times 20$.
prominent rounded, longitudinal folds, separated by a median groove. These folds are covered with a ciliated epithelium of small, compact cells, but in the groove the cells become deeper and less compact, with unusually long cilia. Gland-cells situated below the duct and on each side of it.

Nerve-ring surrounding the œesophagis behind the buccal mass, and too small to allow the buccal mass to be retracted through it.

Cerebral ganglia situated as much at the sides of the œesophagus as above it, and having well-developed accessory lobes. The sensory nerves to the upper tentacles, and the two pairs of peritentacular nerves arise from the cerebral ganglia in front of the accessory lobes; from behind them there arise the nerves to the lower tentacles, the labial nerves, a pair of slender nerves to the two divisions of the buccal retractor, the penial nerve
from the right cerebral ganglion, and the three pairs of connectives. The cerebral commissure is broad, rather long, and arched, and a sub-cerebral commissure also appears to be present.

Buccal ganglia apparently double, each being divided by a transverse furrow into an outer and an inner lobe. Nerves to the œsophagus, salivary glands, etc., arising on each side from the anterior angle of the outer lobe near the end of the cerebro-buccal connective. Odontophoral nerves arising from the inner posterior side of the inner lobe of each ganglion. Buccal commissure rather short, uniting the inner lobes of the ganglia.

Cerebro-pedal and cerebral-pleural connectives shorter than usual. Pedal ganglia longer than broad, united by two short commissures, and closely contiguous excepting in front, where they diverge slightly. They are divided by slight transverse grooves into three or four apparent segments, of which the most anterior pair is the largest. Each ganglion gives off from its lower surface a longitudinal row of about six pedal nerves, the last pair being very large and passing straight backwards through the bodycavity to the hinder part of the foot. The nerves to the sides of the neck arise laterally near the short pleuro-pedal connectives. No otocysts were found.

Pleural and visceral centres very closely aggregated, but the five ganglia distinguishable from one another. Right parietal ganglion twice the size of the left; from each arises a pallial nerve. The two principal nerves arising from the abdominal ganglion were traced as far as the region of the anus, and the upper part of the common duct of the reproductive organs, respectively. Some of the cells of the visceral ganglia are very large, as is often the case, one at the posterior end of the abdominal ganglion being nearly 25 mm . long.

Jaw broad, 2.3 mm . long (when flattened), thin, and smooth, excepting for the fine lines of growth and some traces of very delicate transverse striæ, but having a large, blunt, projecting angle in the centre.

Radula measuring about $4.1 \times 1.9 \mathrm{~mm}$. when flattened out. Central and lateral teeth tricuspid, with rather long mesocones, and short, separate ectocones, the outer edges of which are sometimes slightly serrated. Endocones of lateral teeth rather narrow, and attached to the mesocones excepting just at the point. Marginal teeth five times as numerous as the laterals, aculeate, and mainly unicuspid. Mesocones of marginal teeth very long, except in the last eight or nine teeth, and only very slightly curved. In the first two or three marginals, and in several of the teeth towards the outer edge of the radula, the ectocone is represented by a small projection on the outer side of the mesocone near its base; but in most of the marginals the ectocone as well as the endocone is entirely absent. Bases of teeth
somewhat quadrate, with concave outer edges; narrower in the marginal than in the lateral teeth, but rather short in comparison with the length of the cusps. Rows of teeth nearly straight in the admedian area, there being only a very slight angle in the centre, but trending forwards on each side in the region of the marginal teeth. Radular formula: $(45+9+1+9+45)$ $\times 98$.
Alimentary Canal.-Buccal mass large and muscular, the extremity of the radula-sac projecting slightly from its hind end. Esophagus short, and having, in the specimen examined, a dorsal, backwardly directed pouch at the point where it bends down to pass under the cerebral commissure. Crop nearly twice as broad as the œesophagus, with a projection on the left side at its front end. It passes backwards, without any constriction, into the long and broad, thin-walled stomach. The hind end of the stomach bends down, and from it the intestine passes forwards almost to the heart and then runs back again, describing the usual S-shaped curve, finally passing forwards as the rectum to the anus.

Salivary Glands rather large, situated above and at the sides of the posterior half of the crop, separate from each other in front but joining above the crop further back. Salivary ducts rather long, issuing from the inner sides of the anterior ends of the glands.

Liver consisting of a posterior division, which is smaller than usual and occupies the spire beyond the stomach, and an anterior division to the left of the stomach, which is partially divided into three lobes, one lying in each of the two loops of the intestine and one situated chiefly behind the posterior loop, but sending forward a narrow prolongation between the stomach and the rectum. Hepatic ducts opening into the hinder part of the stomach.

Free Retractor Muscles consisting of four main bands, separate practically from their origin on the columella: the buccal retractor, the right and left tentacular retractors, and a muscle that runs along the right side of the animal just within the bodywall, in which it is inserted near the head. Buccal retractor bifurcating some distance behind the buccal mass, the two divisions being inserted in the right and left sides of its hinder end, and being separately innervated from the corresponding cerebral ganglia. The right division is broader than the left, possibly because it lies in a more direct line between the buccal mass and the columella. Tentacular retractors each dividing further forward than the bifurcation of the buccal retractor into a large muscle inserted in the upper tentacle and a smaller one inserted in the lower tentacle on the same side. Retractor of the right upper tentacle passing between the penis and the vagina. Penial retractor very short, passing from the front of the diaphragm to the posterior end of the penis. No free pedal retractors occur in the body-cavity.

Reproductive Organs.-Hermaphrodite gland consisting of a large number of very small follicles embedded in the posterior division of the liver. Hermaphrodite duct convoluted and somewhat swollen during the greater part of its course, bearing a sub-cylindrical vesicula seminalis at its anterior end. Albumen gland very large. Common duct contorted, and divided, as usual, into an opaque prostatic portion, and a more voluminous, translucent, female portion or uterus. Free oviduct long, the posterior part sacculated. Receptaculum seminis or spermatheca large, elongate, with very thin walls. Receptacular duct with thicker walls, unbranched, and short, being about half the length of the free oviduct. Vagina also short, and without any appendages.

Vas deferens somewhat broader than usual, with a sacculated or closely convoluted appearance as it passes forwards beside the free oviduct. As it bends round towards the penis it is narrower, but it then enlarges again rather abruptly to form a well-marked epiphallus, the walls of which are full of small, opaque white, calcareous glands. The upper end of the epiphallus winds half round the top of the penis before entering it. No flagella or other outgrowths of the male ducts are present.

The calcareous material within the epiphallus consists of innumerable microscopic granules, varying in length from 002 to 006 mm ., and usually slightly less than half as broad as they are long. They are, as a rule, of a rather narrow oval form, but some are more irregular in shape, often having the appearance of being double; while here and there they are aggregated to form small concretions which may exceed 015 mm . in diameter.

Penis rather large, being about 5 mm . long and swollen towards the middle. The posterior end has the form of a knob separated from the remainder by a slight constriction, and into this knob the epiphallus enters and the short penial retractor is inserted. Longitudinal rows of minute papillæ line its walls internally, and it contains a small penis-papilla. The walls of the remainder of the penis have a quite different structure, possessing internal longitudinal folds, two of which are larger and more regular than the others.

Genital atrium very short, and bearing, in addition to the penis and vagina, an amatorial organ, about 3.5 mm . in length, and having an internal structure rather like that of a sponge.

No spermatophore was found.
Spermatozoa having both the head and the proximal part of the tail spirally twisted. Head rather narrow, sharply pointed in front, smooth, and larger than usual, being 009 mm . in length. Tail slender, more than 25 mm . long, its proximal part being furnished with a very narrow spiral flange.

## Helicarion cryptophallus, n.sp.

## Nairobi (?), British East Africa. <br> PLATE IV.

Shell depressed-globose, paucispiral, narrowly rimate, yellowish-green, glossy, translucent, and extremely thin, the greater part of the shell being almost membranous and quite flexible when moist. Spire a little raised ; apex rounded. Whorls $2 \frac{3}{4}$, rapidly increasing, rounded at the periphery. Protoconch composed of $1_{4}^{1}$ whorls, spirally punctate, that is to say, ornamented with spiral rows of minute circular depressions. Remaining whorls almost smooth, excepting for the ill-defined lines of growth, though showing traces of very minute spiral striæ when viewed through the microscope. Periostracum of last whorl not always reaching quite to the suture, but leaving next to it a very narrow lighter band. Suture shallow, not describing a regular spiral, owing to the fact that the top of the first half of the last whorl overlaps the spire to a slightly greater extent than does the top of the penultimate whorl, so that the protoconch has the appearance of being slightly tilted to the left. Aperture transversely oval, about $7 \cdot 5 \mathrm{~mm}$. broad. Peristome simple, very thin, slightly reflected over a narrow rima at its junction with the penultimate whorl. Columella describing a narrow hollow spiral. Altitude 6.3 mm ., breadth 11.3 mm .

The shell of another specimen was slightly larger and its spire more raised, the measurements of this example being : altitude 8.5 mm ., breadth 13.25 mm .

Fоot long and narrow, the hinder part somewhat compressed laterally, the top being flattened beneath the shell, but bluntly keeled for the last 3 mm ., and ending in a short, obtusely pointed projection overhanging the large caudal mucous pore, the opening of which is diamond-shaped. Sole attaining a length of about 8 mm . and a maximum breadth of about 3 mm . in alcohol ; tapering near the hind end, but rounded at the extremity ; tripartite by a pair of longitudinal grooves, the central area being slightly narrower than the lateral areas, especially at the hind end, where the grooves converge. Foot-fringe and lateral areas of sole crossed by numerous transverse grooves. Peripodial grooves well marked, curving upwards at the hind end in front of the caudal mucous pore. A median longitudinal groove is present beneath the shell, but does not extend to the hind end; it gives rise to oblique radial grooves sloping down towards the foot-fringe.

Sides of foot sparsely mottled with dark patches and spots, especially towards its hind end. Most of these dark patches occur along the course of the peripodial grooves, and in a pair of illdefined dark bands that are present towards the hind end of the foot, one on each side of the median dorsal zone, which is
unpigmented. Lateral areas of sole sometimes faintly mottled, but not the central area.

Head and Neck having a darkly pigmented band on each side. A pair of dorsal grooves is present on the neck, but no vertical facial grooves occur on the front of the head, which is covered with very small rugæ. A well-marked oblique lateral groove occurs on each side, the genital opening being on the right lateral groove on the side of the head, about 1.75 mm . from the right upper tentacle. Labial palps rather large.

Pallial Lobes well developed, slightly granular, and spotted with small patches of dark pigment. Shell-lobes wide and rounded, but rather widely separated from each other, the right being about 4 mm . long and almost the same breadth (in alcohol, but probably larger in life), and the left being somewhat smaller. Body-lobes broad, the left extending uninterruptedly from the respiratory opening to a little behind the base of the left shell-lobe, and attaining a remarkable breadth over the animal's neck, which it covers more or less completely.

Dorsal Skin lining the shell translucent and colourless over the lung, kidney, and pericardium, excepting for a trace of brown pigment over the front end of the kidney, but mainly opaque white over the upper part and left side of the liver and adjacent organs, though showing some irregular translucent patches, through which the dark liver is visible.

Lung short, broad near the mantle-edge, but becoming narrower behind, the upper edge receding from the suture. Roof of lung richly vascular, a little more so even than in H. gomesianus. Main pulmonary vein receiving numerous branches just in front of the kidney, and a large branch from the left side of the lung as it enters the pericardium. The largest of the afferent veins is situated in front of this branch. A much smaller branched vein, from the lower surface of the kidney, also unites with the main pulmonary vein close to the heart. Numerous short veins cross the narrow area to the right of the kidney, and can be clearly seen from the outside through the roof of the lung.

Heart large, the auricle being larger than the ventricle.
Aorta dividing into two vessels just after leaving the pericardium. The posterior passes backwards and supplies blood to the liver, etc. ; the anterior, which is the larger, bends round the intestine and a small part of the anterior division of the liver, and passes forwards to the ventral ganglia, giving off on the way a branch on the left to the salivary glands, and one on the right to the body-wall immediately below the anus.

Kidney sigmurethrous, thick and rather narrow, though broadening somewhat at the posterior end; about 6 mm . long, and extending about 2 mm . in front of the heart; containing very numerous folds of a brown colour. Primary ureter very broad
towards its anterior end, which is not so much curved as in H.gomesianus; lined by an irregular network of folds. Secondary ureter extending to the neighbourhood of the anus, and containing numerous transverse folds.

Pedal Gland embedded in the muscles of the upper part of the foot, and only separated from the body-cavity by a thin layer of transverse muscles, through which the gland shows as a pair of longitudinal light-coloured bands divided by a darker median line, the light bands being formed by the glandular tissue, and the dark line by the duct which runs along the centre of the top of the gland. Transverse sections show a similar structure to that found in H. gomesianus, excepting that the median groove in the floor of the duct seems to be deeper and the folds on each side of it somewhat higher.

Nerve-ring surrounding the œsophagus, too small to allow the buccal mass to be retracted through it, and closely resembling that of $H$. gomesianus.

Cerebral ganglia having well-developed accessory lobes, and giving rise to the paired olfactory, optic, and peritentacular nerves in front, to the single penial nerve, and the paired labial and lower tentacular nerves more laterally, and to a pair of slender nerves innervating the buccal retractor, which arise close to the origin of the cerebro-pleural connectives. Both pairs of labial nerves are slightly larger than usual, being quite as thick as the penial nerve, and not much thinner than the olfactory nerves and those to the lower tentacles. The cerebral ganglia are situated somewhat laterally as in H. gomesianus, and are united dorsally by an arched cerebral commissure, and ventrally by a more slender sub-cerebral commissure, which passes down each side near the cerebro-pedal connective, and crosses over the dorsal surface of the pedal ganglia.

Buccal ganglia bilobed, though not quite so conspicuously as in H. gomesianus. Five or six pairs of nerves to the œsophagus, salivary glands, etc., arise from each buccal ganglion near the end of the cerebro-buccal connective, one being united with the connective for a short distance. Odontophoral nerves consisting of one pair of rather thick nerves, and another thinner pair, which arise from the inner sides of the buccal ganglia at the origin of the buccal commissure, and a third pair of still more slender nerves arising from the commissure itself, which is of moderate length.

Cerebro-pedal and cerebro-pleural connectives shorter than usual. Pedal ganglia rather more rounded than in H. gomesianus, but showing the same slight traces of segmentation on the lower surface, and giving rise to the pedal and cervical nerves in a similar manner. Pleural, parietal, and abdominal ganglia closely aggregated, but not united, giving off the same nerves as in the
last species. Genital nerve having a branch to the posterior end of the diaphragm.
Jaw broad, 1.9 mm . long (when flattened), thin, nearly smooth, but crossed by very fine transverse striæ in addition to the equally fine lines of growth. Median projection broad and very low.

Radula measuring about $4.7 \times 2.2 \mathrm{~mm}$. when flattened out. Central and lateral teeth tricuspid, with shorter mesocones than in the $H$. gomesianus. Their ectocones are short and quite separate from the mesocones; the endocones are narrow and poorly developed, being united with the mesocones along the whole length of their inner sides. Marginal teeth very numerous and very close to one another, gradually decreasing in size from the transitional teeth to the edges of the radula. Endocones absent on the marginal teeth ; ectocones almost as long as the mesocones, with which they are united for the greater part of their length. The bifid cusps thus formed are strongly curved, and have their outer edges serrated, this serration becoming more and more pronounced towards the outer limits of the radula, so that, while the inner marginal teeth might be described as bicuspid, the outer marginals would be better described as multicuspid. Bases of marginal teeth narrow, about two-thirds of the length of the cusps ; bases of the other teeth broader, with concave outer edges. Rows of teeth obtusely angled in the centre, whence they trend slightly forwards on each side. The total number of teeth is more than twice as great as in H. gomesianus, the radular formula being: $(86+14+1+14+86) \times 128$. In order to compensate for the small size of the outer marginals, a few short additional rows of these teeth are intercalated at the edge of the radula.

Alimentary Canal.- Buccal mass large, the extremity of the radula-sac projecting from its hind end. Esophagus rather short, thin-walled, with internal longitudinal folds; sometimes swollen into a dorsal, backwardly directed pouch at the point where it bends down to pass under the cerebral commissure. Crop large, about 2 mm . in diameter, its front end projecting forwards on the left side. The anterior part of the crop has rather thick walls with internal transverse folds; the hinder part passes imperceptibly into the large, elongated, thin-walled stomach. This in turn gives rise to the thin-walled intestine, which describes the usual S-shaped curve, before passing forwards as the rectum, in the same manner as in the last species.

Salivary Glands broad, about 4 mm . long, and united with each other above the crop, a large portion of which they cover, although they do not usually reach quite to its front end. Salivary ducts of the usual form.

Liver consisting of a posterior division behind the stomach, and a rather extensive anterior division, in which the loops of
the intestine are embedded, and which is partially divided by them into three main lobes, the most posterior of these lobes sending forward an unusually large prolongation between the stomach and the rectum. Hepatic ducts opening into the hinder part of the stomach, the anterior duct being rather large.

Free Retractor Muscles.-Buccal retractor united with the left tentacular retractor for a short distance posteriorly, bifurcating in front, the two branches being shorter than in H. gomesianus but similarly innervated. Tentacular retractors separate from their origin, dividing fairly far forward into the muscles of the upper and lower tentacles, but giving off no branches to the foot. Retractor of right upper tentacle passing between the penis and the vagina. The so-called tail-retractor is short and not separated from the body-wall, but it gives off a muscle which passes forwards along the right side of the body-cavity and is inserted in the skin near the head. Penial retractor short, passing from the diaphragm to the epiphallus.

Reproductive Organs.-Hermaphrodite gland large, consisting of numerous very small follicles embedded in the posterior division of the liver, as in $H$. gomesianus. Hermaphrodite duct slightly swollen and very much convoluted throughout the central part of its course, bearing a rather small, subcylindrical vesicula seminalis at its anterior end. Albumen gland not very large in the specimens examined. Common duct somewhat contorted, especially towards its hinder end; prostate gland well developed, extending far forwards. Free oviduct short and rather narrow. Receptaculum seminis or spermatheca moderately large, spherical, and thin-walled; situated beside the middle of the common duct. Receptacular duct unbranched, long and broad, with unusually thick muscular walls, longitudinally folded within. Vagina very short, without appendages.

Vas deferens slender excepting towards its posterior end, where it is somewhat broadened, slightly convoluted near its junction with the epiphallus beside the anterior end of the penis. Both vas deferens and epiphallus longitudinally folded within, but not so strongly as the receptacular duct. Epiphallus long, divisible into two portions-a rather thin-walled portion, running backwards beside the penis-sheath to just beyond its posterior end, and a slightly broader, more muscular portion, which first runs forwards for a very short distance, and then doubles back, finally passing forward again into the penis-sheath, which conceals the rest of its course. Penial retractor muscle inserted in the more muscular division of the epiphallus just before it enters the penissheath. Two flagella are borne by the epiphallus, one where its two portions pass into each other not far from the posterior end of the penis-sheath ; the other where the vas deferens passes into the epiphallus, near the anterior end of the penis-sheath. The latter
appendage, which might perhaps be regarded as the true flagellum, is rather long, but much convoluted, and slightly swollen towards its distal extremity; its walls are rather thick and have a gelatinous appearance; its lumen seems to be extremely narrow. The other flagellum, which might possibly be better termed the cæcum, ${ }^{1}$ is also somewhat swollen at the end, butits walls are very thin, and have internal longitudinal folds, its lumen is relatively large, and it is not convoluted but curved round usually in a more or less spiral manner.

The thinner-walled portion of the epiphallus, lying between the two flagella, contains a certain amount of chalky material. This consists of minute calcareous granules, varying in length from .0025 to $\cdot 006 \mathrm{~mm}$., and about one-third as broad as they are long. They are of a narrow, oval form, being narrower and more regular in shape than are the calcareous granules in the epiphallus of H. gomesianus, and in the present species they do not show as great a tendency to become aggregated into concretions.

Penis-sheath forming a structure about 5 mm . long, simulating a large swollen penis. When cut open, however, it is seen to have a long muscular tube folded inside it, the tube when straightened out being more than twice the length of the sheath. At about the middle of its length this tube shows a very slight swelling, which marks the beginning of the true penis; posterior to this point the tube consists of a continuation of the epiphallus. When the penis itself is opened it is seen that the slight swelling is caused by the presence of a short penis-papilla, which projects into the anterior end of the cavity of the penis. The walls of the penis are furnished internally with characteristic diagonal folds, which in places show a slight tendency to be broken up into a little papillæ.

Genital atrium comparatively small. Amatorial organ absent.
Spermatophore consisting of a smooth-walled cylinder, about 6 mm . long and 4 mm . in diameter, curved in accordance with the loops of the more muscular division of the epiphallus in which it was found, and having each end drawn out into a narrow filament which was bent back upon the cylindrical portion. Of these two filaments the one arising from the anterior end seemed to be much the longer, exceeding the rest of the spermatophore in length, but consisting simply of a very slender tube, quite smooth excepting for a couple of slight longitudinal ridges running along it, one on each side.

[^1]Spermatozoa having spirally twisted heads, about 006 mm . long by less than 002 mm . broad, apparently slightly flattened laterally, and tapering to a sharp point in front. Tail very long and slender, sometimes attaining a length of no less that 3 mm ., or fifty times the length of the head. Proximal portion of tail (or " middlepiece ") and head both having the appearance of being furnished with very fine spiral striæ. A more conspicuous spiral flange also surrounds the proximal portion of the tail; it is rather broad close to the head, but gradually becomes narrower posteriorly, until it disappears.

## Affinities.

Among the many members of the Zonitidæ that are found in Africa a large number have been named which bear a close general resemblance to the two species just described. But while these forms all have thin paucispiral shells, well-developed pallial lobes, and a long narrow foot ending in a very conspicuous mucous pore, they seem to show much diversity in their more essential characters.

The species found in Natal and the Cape of Good Hope ${ }^{1}$ resemble $H$. cryptophallus in having an epiphallus bearing two flagella, and also in their type of radula; but they appear to differ from that species, as well as from H. gomesianus, in that the cerebral commissure is usually much shorter, the lung is far longer and less richly vascular, the left body-lobe is divided into two portions, and the caudal mucous pore is overhung by a pointed process often of considerable length; moreover, the detailed structure of the epiphallus, etc., seems to be very different. There can be little doubt, therefore, that these South African species are rightly placed in a separate genus from the tropical forms, although it is difficult to understand why they should have been placed by some authorities in as many as four or five different genera, in view of the general similarity of the internal organs of those that have been dissected.

The species occurring in tropical Africa seem to show a much greater diversity, although very little has hitherto been published about their anatomy. The two forms described in this paper rosemble each other closely in their respiratory and nervous systems, but they differ widely in their radulæ and in almost every feature of their genital organs; while they also show less important differences in the jaw, the retractor muscles, the primary ureter, the spermatozoa, the form of the shell-lobes, the coloration of the animal, etc. It can therefore scarcely be doubted

[^2]that they belong to separate sub-genera, and not improbably to distinct genera.

When, however, we try to decide which of the many other species from Tropical Africa should be most closely associated with either of these forms, great difficulties arise, chiefly owing to our lamentable ignorance of their anatomy. Pollonera ${ }^{1}$ and Pilsbry ${ }^{2}$ have figured the reproductive organs of $H$. aloysiisabaudice, and they closely resemble those of $H$. gomesianus; but an examination of a slightly immature specimen of that species in the British Museum shows that this resemblance does not extend to the other organs ; for in H.aloysii-sabaudice the cerebral and buccal commissures are extremely short-very different from those shown in Pl. III, fig. 4- the lung is longer, and the marginal teeth of the radula are of a quite different type, having short curved bifid cusps, rather like those of $H$. cryptophallus although


Fig. 2.-Representative teeth from the radula of Helicarion aloysii-sabaudice, Poll., Bumaks Island, Victoria Nyanza.- $\times 200$.
the teeth are not so narrow and crowded, the formula being $(31+19+1+19+31) \times 110$. H. aloysii-sabaudice therefore appears to belong to a separate group of these snails. According to Thiele, ${ }^{3}$ H. plicatulus, Mts., H. sowerbyanus (Pfr.), and possibly H. masukuensis, Smith, also have genital organs like those of $H$. gomesianus, while the same seems to be true of $H$. medjensis (Pilsbry), ${ }^{4}$ but without further knowledge of their anatomy it is impossible to say whether these forms are more nearly related to H. gomesianus or to H. aloysii-sabaudice. Externally, H. plicatulus seems to differ from both these species in having a dark band on each side of the animal's neck ${ }^{5}$ and a protoconch without any trace of spiral sculpture, ${ }^{8}$ while $H$. medjensis and $H$. masukuensis are also stated to have smooth embryonic whorls. In H. welwitschii (Morelet) the radula approaches that of $H$. gomesianus more nearly

[^3]than does that of $H$. aloysii-sabaudice (judging from Thiele's figure), and this is also true of $H$. nyasanus, Smith; but in both these species the reproductive system lacks an amatorial organ as well as the flagella.

Several of the other species described by Thiele and Pilsbry, such as H. bequaerti, Pilsbry, H. entagaricus, Pilsbry, H. insularis, Thiele, H. kivuensis, Thiele, H. niger, Pilsbry, H. ruwenzoriensis, Pilsbry, H. schubotzi, Thiele, H. subsucculentus, Pilsbry, and $H$. succulentus, Mts., resemble H.cryptophallus in having an epiphallus bearing two flagella ; but all these species, except $H$. schubotzi and $H$. subsucculentus, differ from H. cryptophallus in possessing a dart-sac ; and in H. schubotzi neither the male organs nor the shell-lobes seem to resemble those of $H$.cryptophallus at all closely, while $H$. subsucculentus cannot be very nearly related to that species since it has a smooth protoconch. The descriptions of Thiele and Pilsbry, however, are insufficient to enable one to judge of the precise affinities of these species.

In the various forms mentioned above the shell has reached about the same stage of degeneration as in the two species described in this paper. But there are several other forms occurring in Tropical Africa in which the shell has become slightly more degenerate, and the shell-lobes are a little broader and united with each other over the front edge of the shell. Of these, H. semimembranaceus, Mts.-of which the reproductive organs and radula have been figured by Thiele ${ }^{1}$-seems to have an epiphallus with two flagella, like $H$. cryptophallus; but it also possesses a large dart-sac, and its radula is of a highly specialized type, with an enormous number of narrow teeth, a specimen in the British Museum which probably belongs to this species having nearly 100,000 teeth, there being about 250 marginals on each side in a transverse row. It is not surprising, therefore, that Pfeffer placed this species in a distinct subgenus, Zonitarion. ${ }^{2}$ The form from Abyssinia, for which Godwin-Austen established the subgenus Africarion, is evidently far removed from both H. gomesianus and H.cryptophallus, as well as from H. semimembranaceus, for it is portrayed as lacking not only a dart-sac and both flagella but also a distinct epiphallus.s Nothing is known of the internal anatomy of $H$. auriformis, Thiele, $H$. haliotides, Putzeys, $I I$. maculifer (Pilsbry), and H. putzeysi (Pilsbry), excepting some of the characters of their reproductive organs. ${ }^{4}$ These species bear

[^4]a certain resemblance to $H$. cryptophallus in possessing flagella on the epiphallus, and $H$. maculifer further resembles that species by having a sheath surrounding the penis and part of the epiphallus but excluding both flagella. Pilsbry states, however, that this species has no penis-papilla, a very important distinction.

The table on p. 107 shows as much as is known about the distribution of some of the more important differential characters among those species that have been dissected.
It is clear, then, that there is much diversity in the anatomy of the species found in Tropical Africa, but until a larger number have been adequately described it would be futile to suggest which of the numerous named forms are the most closely related either to H. gomesianus or to H. cryptophallus. Indeed, in our present state of ignorance it is almost impossible to say how the African Helicarioninæ should be classified, or into how many distinct genera or subgenera they will probably have to be placed. Nevertheless, Pilsbry has recently put forward a tentative classification of the forms with which he is acquainted, "as a basis for further work and criticism." ${ }^{1}$ He suggests grouping the species as follows :-

Genus Africarion, Godwin-Austen. pallens (Morelet).

## Genus Zonitarion, Pfeffer.

 semimembranaceus (v. Marts.) (type).Genus Mesafricarion, Pilsbry. Subgenus Mesafricarion (s.s.).
maculifer, Pilsbry (type), haliotides (Putzeys), auriformis (Thiele). Subgenus Belonarion, Pilsbry. putzeysi, Pilsbry (type).
Genus Helixarion, Fér.
Subgenus Granularion, Germain.
duporti, Germain (type), insularis (Thiele), subsucculentus, Pilsbry. stuhlmanni (v. Marts.), issangoensis (Thiele), volkensi (Thiele).

Subgenus Entagaricus, Pilsbry. entagaricus, Pilsbry (type).
Subgenus Angustivestis, Pilsbry.
niger, Pilsbry (type), bequaerti, Pilsbry, ruwenzoriensis, Pilsbry. succulentus (v. Marts.), kivuensis (Thiele), schubotzi (Thiele).

Genus Gymnarion, Pilsbry.
aloysii-sabaudice (Poll.) (type), (?) sowerbyanus (Pfeiffer), medjensis Pilsbry.

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This classification does not appear to be wholly satisfactory. It is based chiefly on the relative development of the pallial lobes, a comparatively trivial character, which Pilsbry himself admits " is probably of secondary importance ", for nothing is more likely than that these lobes may have undergone parallel enlargement in different genera of the Zonitidæ. Moreover, the various characters which Pilsbry attributes to his genera and subgenera are often not possessed by all the species which he places in those groups. Thus, he describes his subgenus Angustivestis as possessing an oval dart-gland and a shell without a spiral series of punctures on the first whorl, and he also states (in his key) that it has a foot excavated and laterally keeled under the shell. Yet he includes in this subgenus $H$. schubotzi, which, according to Thiele, ${ }^{1}$ has no dart-sac and a punctate protoconch, and H. kivuensis, in which the anterior half of the top of the foot is stated to be only somewhat flattened. Similarly, Pilsbry characterizes his genus Mesafricarion as having a penial sheath, " to which the penial retractor muscle is attached," and as lacking a dart-sac or amatorial organ; and yet his figures of the type species, $H$. maculifer, clearly show that in it the penial retractor is attached to the epiphallus above the penial sheath, as in H. cryptophallus, while in $H$. putzeysi the genital atrium bears a large excitatory organ, which may well be homologous with the dart-sac of $H$. bequcerti, H. semimembranaceus, etc., notwithstanding that it has has become enclosed in a common sheath with the anterior part of the male duct. In the subgenus Granularion Pilsbry places certain forms, some of which have never been described anatomically, but which are said to agree in having the mantlelobes " wholly separated, or only quite weakly united by a narrow rim in front". An examination, however, of Germain's figure of H. duporti, ${ }^{2}$ the type of Granularion, and of d'Ailly's excellent drawings of $H$. pertenuis and the other species which Germain included in his subgenus, ${ }^{3}$ shows that in these forms the pallial lobes are united over the anterior edge of the shell, as in Pilsbry's photographs of $H$. maculifer. ${ }^{4}$ Therefore, although it is, of course, quite possible that $H$. duporti may differ greatly from $H$. maculifer internally, until this has been shown to be the case it would seem best to regard Mesafricarion as a synonym of Granularion, for H. maculifer also agrees with $H$. duporti in having a granulose mantle and a spirally sculptured protoconch. This, however, does not necessarily imply that a new name must be found for the

[^6]group of species with separated shell-lobes, to which Pilsbry has applied the name Granularion, since it has yet to be proved that these forms differ from the others in any really important characters, notwithstanding that Pilsbry has placed them in a distinct genus. Unfortunately, $H$. duporti has never been dissected, and we also know nothing whatever at present about the radula, the nervous system, the cephalic retractors, the pedal gland, the respiratory system, or the excretory organs of any of the species which Pilsbry placed in either Mesafricarion or Granularion. The forms which he assigns to the genus Gymnarion are probably more nearly related to one another than to any of the preceding species; yet the only anatomical feature in which the members of this group seem to differ constantly from the other forms is in the character of the male ducts, and they show much diversity among themselves in other respects.

On theoretical grounds it is not improbable that the resemblance of these African snails to the typical species of Helicarion from the Australian region is largely due to convergence, brought about by the analogous degeneration of the shell and development of the pallial lobes in both regions. But at present there appears to be no justification for assuming that this is actually the case. Helicarion cuvieri, Fér., the type of the genus, seems to be very similar to some of the African forms, not only in its external features, but also in its radula and in its reproductive organs, which bear a single flagellum, ${ }^{1}$ as in $H$. auriformis, Thiele. But whether $H$. cuvieri also agrees with the African species in its other organs awaits further investigation. It would be very interesting to know, for example, whether in the Australian forms the buccal ganglia are bilobed, in the same way as they are, to a greater or less.extent, in all the African Zonitidæ that I have examined. ${ }^{2}$ For the present, therefore, it would seem best to continue placing all the species from Tropical Africa with a paucispiral shell and a large mucous pore in the genus Helicarion.

If, however, it is thought advisable, even in our present state of ignorance, to classify in some way the species from Tropical Africa as a basis for further work and criticism, I venture to think that the following tentative classification of the better known species may possibly prove more acceptable than that proposed by Pilsbry. In each group an attempt is made to arrange the species as far as possible in order, beginning with those that are probably the most primitive.

[^7]
## Genus Helicarion, Fér. ${ }^{1}$ Subgenus Zonitarion, Pfeffer.

Protoconch smooth, without spiral sculpture; remaining whorls usually with microscopical spiral striæ, excepting in some of the species with large shell-lobes. Left shell-lobe narrow or triangular, becoming flattened out into a low straight fold in those forms in which the shell-lobes are united. Right shell-lobe variable in size, often with a median ridge when large. Median projection of jaw low or obsolete. Central and lateral teeth rather narrow, with anteriorly prolonged bases; marginals extremely numerous (in H. semimembranaceus, at least). Epiphallus bearing two flagella, the distal one sometimes of a considerable size. Spermatheca usually somewhat elongated. Genital atrium bearing a muscular dart-sac.

Known distribution: Equatorial Africa, from the borders of Uganda to the west coast.

Section Angustivestis, Pilsbry.
Last whorl of shell spirally sulcate. Shell-lobes narrow and separate.
ruwenzoriensis, Pilsbry.
kivuensis, Thiele.
niger, Pilsbry (type of section).
bequaerti, Pilsbry.

## Section Entagaricus, Pilsbry.

Shell-lobes separate, the right broadly rounded, the left triangular. Dart-sac mushroom-shaped.
entagaricus, Pilsbry.

## Section Belonarion, Pilsbry.

Shell-lobes concrescent, the right broad, the left triangular. An excitatory organ ( = dart-sac ?) is included in the penial sheath, which reaches the retractor muscle.
putzeysi (Pilsbry).

## Section Zonitarion, s.s.

Shell-lobes concrescent, the right broadly rounded with a median ridge, the left reduced to a low straight fold. A penial sheath apparently extends to the retractor muscle.
haliotides, Putzeys.
semimembranaceus, v. Marts. (type).

[^8]
## Subgenus Granularion, Germain.

Protoconch spirally punctate (excepting in H. subsucculentus), often having the appearance of being slightly tilted to one side; remaining whorls glossy, with little or no microscopical spiral sculpture. Shell-lobes usually rather more granular than in the last subgenus, the left broad and nearly always rounded, the right more variable, hut never ridged, often more or less concrescent with the left. Medium projection of jaw present, but usually rather low. Central and lateral teeth normal, marginals numerous. Epiphallus bearing two rather small flagella, rarely reduced to one. Penial sheath when present not extending to the retractor muscle. Spermatheca usually spherical. Genital atrium not bearing a dart-sac, which is either absent or takes the form of a hemispherical protuberance at the junction of the vagina and oviduct.

Known distribution: Equatorial Africa, from British East Africa to the west coast, and extending northwards into the Sudan.
> succulentus, v. Marts. stuhlmanni, v. Marts. ${ }^{1}$ insularis, Thiele. schubotzi, Thiele. subsucculentus, Pilsbry. cryptophallus, n.sp. columellaris, d'Ailly. duporti, Germain (type). pertenuis, d'Ailly. issangoensis, Thiele. maculifer (Pilsbry). auriformis, Thiele.

Subgenus Africarion, Godwin-Austen.
Shell-lobes rounded, concrescent, with a dark band on the left side. Median projection of jaw rather small, but prominent. Central and lateral teeth normal, marginals not very numerous. Spermatheca spherical. No flagella, epiphallus, or dart-sac.

Known distribution : Abyssinia.

$$
\text { pallens, Morelet (?). }{ }^{2}
$$

[^9]
## Subgenus Gymnarion, Pilsbry.

Protoconch smooth, or more usually spirally punctate (though apparently on a rather smaller scale than in Granularion) ; remaining whorls very finely microscopically granulate, except on the base. Shell-lobes narrow, separate, and usually quite small. Median projection of jaw prominent. Central and lateral teeth normal, marginals variable in form but never very numerous. Epiphallus present, but flagella absent. Penis ending in a slight knob, into which the epiphallus enters and the retractor muscle is inserted. Spermatheca usually oval, with a comparatively short duct. Genital atrium often bearing an elongated non-muscular amatorial organ.

Known distribution: Equatorial Africa, from Uganda to the west coast, and extending in a southerly direction into Rhodesia and Portuguese East Africa south of the River Zambesi, which is much further south than the other subgenera are at present known to extend.

> plicatulus, v. Marts. aloysii-sabaudia, Poll. (type). sowerbyanus (Pfeiffer). gomesianus (Morelet). welwitschii (Morelet). nyasanus, Smith. masuliuensis, Smith. medjensis, Pilsbry.

Further investigation will probably show that this group should be separated generically from Zonitarion and Granularion, and just possibly from Africarion also ; and it will almost certainly have to be subdivided into two or three subgenera or sections. The species here placed in the subgenus Granularion also appear to belong to two or three different sections, but so little is known about their anatomy that it is not yet possible to say how they should be classified. Pilsbry has well said that at present most of the African species of Helicarion form a " nearly meaningless mass of materials which nobody can utilize until the descriptive work is all done over from a different standpoint".

[^10]
[^0]:    ${ }^{1}$ Vitrina gomesiana, Morelet, Voy. Welwitsch, Moll. terr. et fluv., 1868, p. 52, pl. i, fig. 2.
    ${ }^{2}$ The shell was not in sufficiently good condition to enable me to describe its microscopical sculpture in greater detail.

[^1]:    ${ }^{1}$ This appendage corresponds to that which Pilsbry terms the "lime gland"; but in the forms with which I am acquainted it seems to be neither glandular nor calcareous, the chalky granules in the epiphallus occurring chiefly towards the base of the other flagellum. I therefore prefer GodwinAusten's terminology.

[^2]:    ${ }^{1}$ See Pilsbry, Proc. Acad. Nat. Sci. Philad., 1889, p. 279, pl. ix ; and Godwin-Austen, Ann. \& Mag. Nat. Hist., ser. viii, vol. i, 1908, pp. 131-133, pl. viii ; vol. ix, 1912, pp. 122-139, 569-585, pls. i-vii, xii-xvii; vol. xiii, 1914, pp. 449-472, pls. xix, xx.

[^3]:    ${ }^{1}$ S'pedizione al Ruwenzori di Princ. Luigi Amadeo di Sovoia, vol. i, 1909. pl. iii, fig. 15.

    2 Bull. Amer. Mus. Nat. Hist., vol. xl, 1919, p. 277, fig. 140.
    ${ }^{3}$ Deutsch. Zentral-Afrika-Exped. (190'7-08), vol. iii, 1912, pp. 189-199, pl. vi.
    ${ }^{4}$ Bull. Amer. Mus. Nat. Hist., vol. xl, 1919, pp. 277-278, fig. 142.
    5 Von Martens, Monatsbr. Akad Wissensch. Berlin, vol. xxvii, 1876, pl . i, fig. 5.
    ${ }^{6}$ D'Ailly, Bihang K.Sv. Vet.-Akad. Handl., vol. xxii, pt. 4, 1896, p. 30.

[^4]:    ${ }^{1}$ Deutsch. Zeniral-Afrika-Exped. (190\%-0S), vol. iii, 1912, p. 190, fig. xi; pl. vi, fig. 59. (Pilsbry is mistaken in saying that the genital organs of this form have not been figured.)
    ${ }^{2}$ Jahrb. Deutsch. Malak. Gesell., vol. v, 1878, pp. 275-6 ; Abhandl. Gebiete Naturwiss. Hamburg, vol. viii, pt. 2, 1883, pp. 4, 8, 9, 11.
    ${ }^{3}$ Godwin-Austen, Mollusca of India, vol. i, 1883, pp. 154-6, pl. xlii.
    ${ }^{4}$ Thiele, Deutsch. Zentral-Afrika-Exped, (1907-08), vol. iii, 1912, p. 198 ; Pilsbry, Bull. Amer. Mus. Nat. Hist., vol. xl, 1919, pp. 259-64, figs. 122, 124, 127.

[^5]:    ${ }^{1}$ Bull. Amer. Mus. Nat. Hist., vol. xl, 1919, pp. 258-278.

[^6]:    ${ }^{1}$ Deutsch. Zentral-Afriía-Exped. (190y-0S), vol. iii, 1912, p. 194.
    ${ }^{2}$ Bull. Mus. Paris, 1912, p. 257, fig. 58.
    ${ }^{3}$ Bihang K. Svensk. Vet.-Akad. Handl., vol. xxii, pt. 4, 1896, pls. i, ii.
    ${ }^{4}$ Bull. Amer. Mus. Nat. Hist., vol. xl, 1919, pl. xxii, figs. 1, $1 a, 2$. H. issangoensis, another species included by Pilsbry in this subgenus, also has fairly broadly connected pallial lobes, according to Thicle.

[^7]:    ${ }^{1}$ Semper, Reis. im Arch. Philipp., Thl. II, vol. iii, 1870, p. 31, pl. iii, fig. 7; pl. vi, fig. 11; Thiele, Deutsch. Zentral-Afrika-Exped. (190'y-08), vol. iii, 1912, p. 190, pl. vi, fig. 57.

    2 The buccal ganglia do not appear to be bilobed in H. kuekenthali, Kob., from the Island of Halmahera (Wiegmann, Abhandl. Senckenb, naturf. Gesell., vol. xxiv, 1898, pl. xxii, fig. 21).

[^8]:    ${ }^{1}$ On pp. 19 and 20 (or 23 and 24) of Férussac's Tabl. Syst. Anim. Moll., Fam. des Limaçons, 1821, this word is misspelt Helixarion ; but on p. 67 (or 71) of the same work Férussac himself corrected this blunder, and it would seem to be a pity to ignore his correction, as Pilsbry has done.

[^9]:    ${ }^{1}$ The species referred to in this paper as $H$. stuhlinanni, v. Marts., is that described as such by Thiele (Deutsch. Zentral-Afrika-Exped. (1907-08), vol. iii, 1912, pp. 194-195, pl. vi, fig. 64). But Thiele states that his examples have neither the microscopical spiral striz seen in the type-specimen, nor the coarse furrows that von Martens describes as characteristic of his species. Moreover von Martens states that the animal is dark grey (in alcohol), and that its right shell-lobe is triangular (Deutsch-Ost-Afrika, vol. iv, 1897, p. 37), while Thiele describes the animal as of a light colour, with rounded pallial lobes. It therefore seems possible that the form described by Thiele is not identical with von Martens' species.
    ${ }^{2}$ The Abyssinian form described by Godwin-Austen (Moll. of India, vol. i, 1883, pp. 154-6, pl. xlii) is at present the only species known to belong to the

[^10]:    subgenus Africarion, and its identification with $H$. pallens, Morelet, is still not quite certain. The two Indian species which Godwin-Austen at one time also placed in Africarion differ considerably from any of the African forms, and are now placed in the genus Pseudaustenia, Cockerell (see Blanford and Godwin-Austen, Fuuna of Brit. India, Moll. Testacellida and Zonitida, 1905, pp. 206-9). It is possible, however, that $H$. subangulatus, v. Marts., from the Semliki Valley near Mount Ruwenzori, may prove to belong to this subgenus, but at present its anatomy is unknown.

